"On the Interpretation of Photographic Records of the Response of Nerve obtained with the Capillary Electrometer." By George J. Burch, M.A., F.R.S., Physiological Laboratory, Oxford. Received February 11,—Read February 20, 1902.

Preliminary Note.

Attention is specially directed to the following changes in the terms used to describe the electrical phenomena of living tissues :—

Old term.	New term.
Negative phase, or first phase...	Electro-positive phase, or first phase.
Positive phase, or second phase	Electro-negative phase, or second phase.
Galvanometrically negative......	Positive, electro-positive.
Galvanometrically positive	Negative, electro-negative.

This terminology has been advocated for some time by Dr. Waller, who drew attention to it at the International Physiological Congress at Turin, 1901, and is now adopted by Professor Gotch and myself as being more in accordance with the phraseology employed by physicists in similar cases.

In Parts I and II, where the subject is treated from a purely physical standpoint, special terms have been used in order to avoid the confusion that might have arisen owing to the different meanings attached by physiologists to certain words used by physicists.

Thus—

Bundle = Nerve or Muscle.
Linear conductor = Nerve-fibre or Muscle-fibre.
Point of origin = Exciting electrode, &c., or nerve-ending, &c.

In Part III the ordinary physiological terms are employed.

Statement of the Problem.

In previous papers on the capillary electrometer I have shown how it is possible, from the curves obtained by photographing on a rapidly moving plate the excursions of the end of the column of mercury, to draw derived curves representing the variations of the difference of potential by which these excursions were produced.

I have pointed out* that the photographic records obtained when two currents of definite potential difference and opposite in direction, lasting respectively as long as the first and the second phase of the electrical response of muscle, are thrown in succession into the electro-

* 'Phil. Trans.,' A, vol. 183, p. 100.

meter, differ in form from the records of the muscle response. In the former case the movement of the meniscus commences suddenly—the velocity is maximal at the commencement—the change of direction is sudden, and the end of the second phase is sudden also. It is quite otherwise with the records of the electrical response of muscle or nerve. There is great variety in them. The movement generally commences gradually. Maximum velocity may occur early or quite near the end of the first phase. The reversal of direction may be so sudden as to form a cusp, or the curve may be flat-topped for 0·001 sec. or 0·002 sec. The second or electro-negative phase may be cut short, or may exceed the first or electro-positive phase in magnitude. It may end almost abruptly or tail off so gently that it is difficult to determine when it ceases. But so long as the conditions are unaltered the same shaped curve is produced on repeating the experiment.

These varieties among the records are therefore due to characteristic peculiarities of the preparations.

But the characteristic peculiarities of a preparation may depend on the one hand upon its physiological state, and on the other upon purely physical and experimental conditions. It is necessary therefore to trace the influence of these latter on the form of the records, in order, by a process of elimination, to discover the results due to physiological differences.

I propose therefore in the present communication to show that it is possible to obtain further information by applying to the derived curves a process of interpretation based on purely physical grounds, and shall avoid dealing with the physiological side of the question except so far as may be necessary for the sake of clearness.

The first statement of the problem is best made from the experimental standpoint, and may be expressed briefly as follows* :—

* [*Note, added April* 10, 1902.—This is an expression from a purely physical standpoint of the well-known physiological theory of which the experimental basis is in brief:—

1. Du Bois Reymond's demonstration that the excitatory process in nerve is associated with electrical phenomena.

2. The classical experiment of Helmholtz, showing that the excitatory process in motor nerve, as judged by the time of the muscle response, is transmitted along the nerve at a definite rate.

3. Bernstein's proof, by means of his revolving rheotome, that the electrical phenomena are transmitted in the form of a wave at the same rate.

A great deal of work on the subject has been done with the revolving rheotome by Hermann, Bornttau, Hering, and others.

Professor Gotch and I have discontinued the use of the revolving rheotome, because, in the first place, the condition of the nerve is liable to be altered by the rapid series of excitations; in the second place, because the after-effect of each excitation is mixed up with those of succeeding ones; and in the third place, because the capillary electrometer is far more sensitive.

It is this greater sensitiveness that has enabled me to push the investigation so much farther than has hitherto been attempted.]

A source of electromotive force is developed at a given point in a bundle of linear conductors imperfectly insulated from each other, is propagated* in both directions along the bundle, and finally subsides. It is required to investigate the variations of potential difference between any pair of points on the conductors.

Obviously the conditions are extremely complex, and a complete solution is impracticable because, from the nature of the case, it is impossible to determine the amount of the leakage from each conductor into the bundle. It is possible, however, to separate from the results those which depend upon purely physical conditions, and thus to clear the ground for the discussion of the truly physiological phenomena. In analysing photographs taken in this laboratory I have met with illustrations of all the points brought forward in this paper.

In thus dealing with the problem, it is necessary to take the following considerations into account:—

(1.) That the linear conductors (or briefly the conductors) constituting the bundle are not necessarily all of the same length.

(2.) That the electrical change originates in each conductor at a certain point of its length, from which it is propagated simultaneously in both directions.

(3.) That the points at which the electrical change originates in the different conductors may be all situated in the same cross-section of the bundle, or may be distributed along a certain portion or portions of its length.

(4.) That the development, as also the subsidence, of the E.M.F. at any given point of a conductor may conceivably be gradual or sudden, *i.e.*, the change from zero to maximum, or *vice versâ*, may be instantaneous, but is not necessarily so.

(5.) That the time relations and intensity of the electrical change may be temporarily or permanently modified at a given point in any or all the conductors of the bundle.

In stating the problem it is necessary to put it into such a form as will represent these conditions.

The simplest way of doing so is to deal first with the case of the single linear conductor, and to express the electrical changes in it as

* [*Note, added April* 10, 1902.—I can find no exact physical analogue to this phenomenon, and no other single word to express it than this physiological term.

It has been, I believe, compared to the lighting of a train of gunpowder in the middle. The flame spreads outwards in both directions, but dying out first in the middle, separates into two tracts of flame of practically constant length, travelling away from each other.]

the sum of two functions—one representing the development and the other the subsidence of a wave of electromotive force passing along it. Having thus dealt with the single linear conductor, the more complex case of a bundle of conductors may be expressed as the sum of a number of similar functions with different constants.

But although this method of proceeding is convenient for examining the experimental results, it only represents indirectly the facts which it is our object to investigate.

The real problem may be stated thus: Conceive three similar consecutive short portions, A, B, C, of a single nerve fibre, such that each of them may be regarded as a complete element of the fibre; it is required to determine—

1. The development, duration, and subsidence of the electrical changes in either of them.
2. Those conditions in B which enable it to become active under the influence of A.
3. Those conditions in B which enable it to induce a state of activity in C.

It will be observed that 1, 2, and 3 enter simultaneously into almost every possible experiment, but may be separately investigated by two distinct methods, namely, the physical—*e.g.*, alteration of position of leads, exciting electrodes, &c.—and the physiological—*e.g.*, influence of temperature, electrotonus, reagents, injury, &c. But whether the method be physical or physiological, the analysis of the photographic record merely gives the sum of the electrical changes occurring between two fixed electrodes at any given moment, so that in either case the analysis itself has to be interpreted in order to show how the curve is to be explained in terms of 1, 2, and 3.

It will be observed that no assumptions are made either as to the cause of the electrical phenomena, or the mode in which they are related to the activity of the tissue, beyond the fact that there is in muscle or nerve a potential gradient between a part in a state of physiological activity and neighbouring parts at rest. The E.M.F. might, so far as this investigation is concerned, be a function of the active condition, or of the transition from one state to another. In either case the method of dealing with the records would be the same. But having ascertained the meaning of the records, it may be possible by comparing them to determine whether the electrical changes are essential, or merely concomitant phenomena, of the active state.

I. *Variations of Potential Difference between Two Points of a Linear Conductor traversed by a Source of E.M.F.*

In the accompanying diagram (fig. 1) the successive stages of the electrical condition are represented graphically, and arranged in order of time. An electromotive force is supposed to originate at the point P, from which it spreads in both directions, the shaded portions indicating the parts in which it exists, and those not shaded the parts not yet reached by it, or no longer affected. The shaded parts may therefore be considered as positive to the unshaded. After a certain interval the effect subsides. This is represented as occurring first at the point from which it originated. Obviously, if the duration of the active period is the same for each point of the linear conductor, the time curve of the subsidence of the wave of E.M.F. will be parallel to its development. It does not, however, necessarily follow that it must be so, and hence the cessation of electrical activity may be more conveniently represented as a separate function of the time.

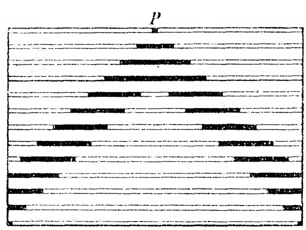

FIG. 1.—Diagram showing the successive positions of a wave of electromotive activity originating at the point P of a nerve-fibre, and travelling outwards in both directions. The shaded portions are positive to the unshaded.

The general effect of varying the rate at which the electrical change is propagated, and its duration in various parts of the linear conductor, is shown in figs. 2 to 7. They are drawn on the same plan as fig. 1, that is to say, time is reckoned from above downwards, and position on the linear conductor horizontally. The excitation is supposed to take effect at the centre of the conductor, and to spread symmetrically to the right and to the left. But in order to show more forcibly the relation between the above-mentioned two modes of expressing the problem, the right-hand half of each figure represents the electrical change as a wave passing along the conductor, while the left-hand half gives the commencement, duration, and end of the electrical activity at a series of points on the conductor.

The relation of the electrical changes to variations of potential difference between any given pair of leads may be studied by drawing a pair of vertical lines the required distance apart on tracing cloth,

and applying them to the diagram so as to represent by their position the position of the leads. The first phase begins when the wave of electrical activity reaches the first lead, and continues until it either leaves the first lead or arrives at the second. The second phase begins whenever the wave has both left the first lead and arrived at the second. But if neither or both the leads are affected by the wave, there is zero potential difference between them.

In fig. 1 the duration of the active period is constant for all parts of the conductor. This involves equality between the rate of propagation and the rate at which the disturbance dies out along the conductor. Both the length of the wave and the duration are constant.

In fig. 2 the velocity of propagation of the development is greater than that of the subsidence of the effect. Both the duration and the wave-length increase regularly. The converse of this is shown in fig. 3, where the wave of development travels slower than that of subsidence, corresponding to a regularly diminishing wave-length and also duration.

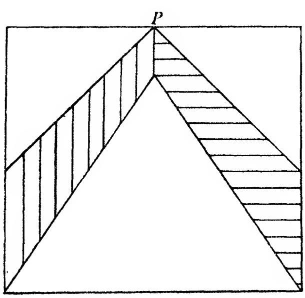

Fig. 2.—As in Fig. 1, but the duration of the active condition increases continually, as indicated by vertical lines on the left side. This corresponds to an increasing length of wave, as shown by the horizontal lines on the right.

N.B.—Time is measured vertically downwards, and position on the nerve-fibre horizontally.

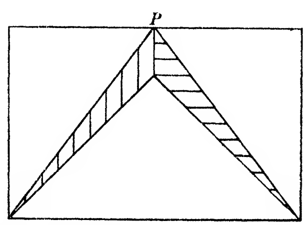

Fig. 3.—As in Fig. 2, but the duration continually diminishes (left side), corresponding to a continually diminishing wave-length (right side).

Manifestly under such conditions the response would not be propagated beyond a limited distance. I have some reason for believing that responses of this character might be obtained from kept muscle with minimal stimuli.

Up to this point there has been no marked difference between the two ways of representing the problem. With fig. 4 it is otherwise. Here the rate of propagation is constant, but the duration, as shown

on the left side, suddenly increases at a certain point from 3 to 5 units. Regarded as a wave of electrical activity, this *sudden* change is equivalent, as the right side of the figure shows, to a *gradual* increase of wave-length to a new constant value.

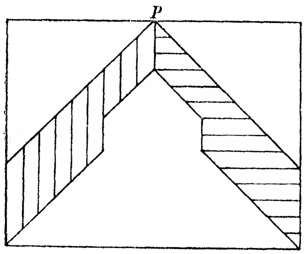

FIG. 4.—A sudden definite increase of duration (left side) implies a gradual transition from a constant short wave to a constant long wave (right side).

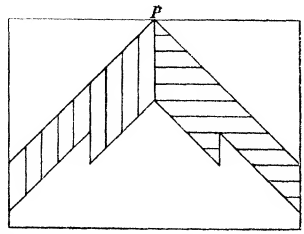

FIG. 5.—A sudden definite diminution of duration (left side) corresponds to a separation of the wave of activity for a short time into two portions (right side).

Fig. 5 is the converse of fig. 4, the duration suddenly diminishing at a certain point from 5 to 3. This diagram brings out the curious result that under these conditions the wave may split up into two portions. Moreover, for certain positions of the leads, the record in such a case would be monophasic.

Figs. 6 and 7 show the effects of a change in the rate of propagation, unaccompanied by any change in the duration. Two things should be noticed—first, that the slower rate of propagation corresponds to a

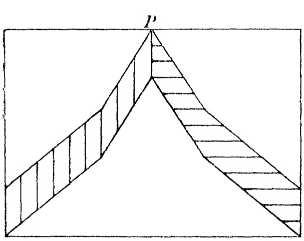

FIG. 6.—A sudden definite increase in velocity of propagation, the duration remaining constant (left side), involves a gradual increase of wave-length from one fixed value to another (right side).

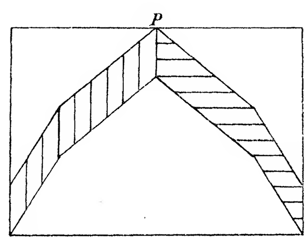

FIG. 7.—A sudden definite decrease in velocity of propagation, the duration remaining constant (left side), involves a gradual shortening of the wave from one fixed length to another.

shorter wave unless the duration is increased in the same proportion, and farther, that whereas the change of rate is sudden, the change of wave-length is gradual.

Problems of this type arise when two portions of the same nerve are kept at different temperatures. They may be worked out graphically, or by writing a separate formula for each portion where a sudden change occurs.

Proceeding to a closer examination of the problem, it will be convenient to consider in the first place the variations of P.D. due to the propagation of the wave-front of electrical activity. It may be assumed provisionally that its rate of propagation is constant, and that its passage is marked by a sudden definite rise of potential. As a farther simplification, the linear conductor is assumed to be of indefinite length, the origin of co-ordinates being situated to the left of the portion under consideration, so that the position of each of the leads connecting it with the electrometer may be represented by a positive quantity.

Let the line ON, fig. 8, represent a linear conductor of indefinite length, and let P be the point at which the electrical change originates.

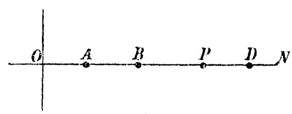

FIG. 8.—Needs no explanation, save the text.

Let the distance OP $= p$. Let leads connecting ON with an electrometer be placed at any two of the points A, B, or, D, and let their respective distances from O be a, b, d.

Let T $= t + s$, be the time that has elapsed since the instant of stimulation, s representing the *latent* period if any exists, and t being the time that has elapsed since the response commenced. In most cases s is eliminated, and therefore t will be used in the formulæ. The exceptions are dealt with on p. 211.

Let x represent the distance from O of the wave-front of the electrical change at the time t. Then $x = p \pm vt$, where v is the velocity of propagation of the wave-front in centimetres per second. The sign of v is positive for all points to the right of p and negative for all points to the left of it.

In the simple case under discussion, namely, that of a sudden definite rise of potential at the wave-front, it is manifest that a difference of potential will be established between A and B as soon as the wave-front has passed B, and that it will cease when the wave-front reaches A, both electrodes being then at the higher potential: *i.e.*, the P.D. begins when $b = p - vt_1$, and ends when $a = p - vt_2$.

Hence $$t_1 = (p-b)/v, \qquad t_2 = (p-a)/v;$$

and the duration of the difference of potential between A and B is

$$t_2 - t_1 = (b-a)/v.$$

Inasmuch as this expression does not contain p, it is evident that the duration of the P.D. between two leads both of which are situated on the same side of P is independent of the position of the point at which the electrical change originates, and is conditioned solely, so far as the wave-front is concerned, by the distance between the two leads. On the other hand, the period of delay between the moment at which an E.M.F. is first established at P, and the commencement of the P.D. between the leads, varies directly with the distance of P from B.

The case is otherwise when leads on both sides of P are taken, *e.g.*, B and D. The wave-front reaches B when $t_1 = (p - b)/v$, and it reaches D when $t_2 = (p - d)/-v$.

Suppose D is nearer to P than B is, this will make a P.D. in the same direction as in the previous example. Then $t_2 < t_1$, and the duration of the P.D. is,

$$t_1 - t_2 = \frac{p-b}{v} - \frac{d-p}{v} = \frac{2p-(b+d)}{v}.$$

Since by the diagram $d > p > b$, we may write $b + k = p$ and $p + l = d$. Then

$$t_1 - t_2 = (k - l)/v.$$

This expression is clearly a maximum when either $k = 0$ or $l = 0$. It will be observed that the sign of the resulting P.D. varies according as k or l is greater. Hence the duration of the P.D. will be greatest when one of the leads coincides with P, zero if P is midway between them, and it will vary in sign according as D or B is nearer to the point at which the E.M.F. originates. The delay will be zero if either electrode coincides with P, and cannot exceed the maximum of $(d - b)/2v$, at which point the duration becomes zero, and the value of the P.D. consequently vanishes.

The next step is to trace the time relations of the P.D. between the terminals which may result from the removal of the source of E.M.F. If the condition of electrical activity after having invaded the whole conductor begins at any moment to subside simultaneously at all points, and if the rate of subsidence is the same at all points of it, no P.D. will be produced between any two points, however situated. If the electrical activity begins to subside before it has invaded the entire conductor, and while the wave-front is still between the two electrometer leads, then if it subsides simultaneously over the whole part affected, the P.D. between the leads will simply fall to zero.

If the electrical activity, after having invaded the whole conductor, subsides first at the two ends of it, persisting longest at P, where it originated, the period of the subsidence will be marked by a second P.D. between the leads, of the same sign as that evoked by the wave-front of electrical change.

But by observation it is found that the first electrical change (in the case of muscle or nerve) is followed by a second in the opposite direction, and therefore we are justified in assuming that the subsidence of the condition of activity in the case of muscle and nerve takes place first at the point at which it originated.

We may therefore designate the position in the linear conductor of the wave-front of cessation from the active condition by an expression of the form,

$$x_1 = p \pm v_1(t+\theta),$$

where θ represents the duration of electrical activity in the portion of the linear conductor under P. If the central portions of the linear conductor remain active longer than those nearer the ends, then $v_1 > v$. If the period of activity becomes longer as the ends are approached we must have $v_1 < v$.

But if under normal conditions each portion of the linear conductor becomes active to the same degree, and for an equal period, then $v_1 = v$, and the progress of the wave of electrical activity must be represented by two parallel curves, one indicating its development and the other its subsidence for successive points along the linear conductor.

Hence in the normal case now under consideration we may put $v_1 = v$. Then, between the leads A and B, B becomes negative to A when the wave of cessation

$$x_1 = p - v\,(t - \theta) \text{ reaches B, } i.e., \text{ when}$$
$$t_1' = (p - b + v\theta)/v,$$

and remains negative to t until the wave-front reaches A, *i.e.*, when

$$t_2' = (p - a + v\theta)/v.$$

The duration of the P.D. is as before

$$t_2' - t_1' = (b - a)/v,$$

the two waves differing only by a time-constant θ.

Taking now the combined effect of both waves, it is evident that the form of the resulting curve of P.D. must depend upon the relation between θ and $(b - a)/v$.

If $(b - a)/v$ is less than θ then the first phase of the effect upon the leads A and B will be over before the second phase begins, and therefore there will be an interval of $\left(\theta - \frac{b-a}{v}\right)$ between them during which the P.D. will be zero.

If $(b-a)/v = \theta$ then the first phase will be succeeded by the second phase with no interval between.

If $(b-a)/v$ is greater than θ then the second phase starts before the first is over, but being of opposite sign, and *ex hypothesi* equal in

intensity, neutralises it and produces zero P.D. for a period equal to $\left(\frac{b-a}{v} - \theta\right)$.

Since the value of $(b-a)/v$ can be varied by shifting the leads A and B, it follows that θ can be determined by ascertaining at what distance between the leads the two phases of the P.D. follow one another without a zero interval between, for the sequence of potential differences will be

(1) With A and B close together,

$$0,\ +,\ 0,\ -,\ 0.$$

(2) With A and B at one particular distance,

$$0,\ +,\ -,\ 0.$$

(3) With A and B far apart,

$$0,\ +,\ 0, -,\ 0.$$

The case of leads on either side of P is similar, the phases of the resulting P.D. varying according to the relation

$$(k-l)/v > \theta;\ 0,\ \pm,\ 0,\ \mp,\ 0.$$
$$(k-l)/v = \theta;\ 0,\ \pm,\ \mp,\ 0.$$
$$(k-l)/v < \theta;\ 0,\ \pm,\ 0,\ \mp,\ 0.$$

II. *Variations of P.D. between Two Points of a Bundle of Linear Conductors traversed by a Source of Electromotive Force.*

Hitherto it has been assumed that the rise of P.D. at the wave-front of electrical activity is sudden, and its fall equally sudden at the end of the wave, and also that the electrical change is not complicated by the structure of the linear conductor in which it occurs.

It is necessary to investigate farther the modifications which may result when a number of such linear conductors act together.

In my paper on the "Time Relations of the Capillary Electrometer,"* I pointed out that in the case of muscle the rise of potential difference at the wave-front is not sudden, and the same is shown with respect to nerve in the analyses published by Professor Gotch and myself. Moreover, in the discharge of the electrical organ of Malapterurus, the E.M.F. is gradually developed, although in this case the phenomenon cannot be accounted for by propagation. There is sufficient evidence to warrant the introduction into the formula of a term expressing gradual development of E.M.F.

In dealing with the phenomena of a bundle of linear conductors, three things have therefore to be taken into account, viz. :—

* 'Phil. Trans.,' A, vol. 183, pp. 100, 104.

A. The points of origin of the wave of activity in the several linear conductors may be differently situated in the bundle.

B. The development of the E.M.F. at any given point of a linear conductor may be gradual, and so also may its subsidence, and the rate of subsidence may be different from the rate of development.

C. The constituent linear conductors may not all extend to both of the leads selected.

A. Influence of the Position of the Points of Origin in a Bundle of Linear Conductors.

Let the points of origin $P_1, P_2, P_3, \ldots P_n$ referred to O as origin of co-ordinates, be $p_1, p_2, p_3, \ldots p_n$.

Fig. 9.—A bundle of linear conductors, connected with the electrometer at any two of the points A, B, D. $P_1 \ldots P_n$ are the points at which the electromotive change originates.

(1.) It is evident that with respect to the leads A and B, the duration of each phase of the effect will be alike for all the linear conductors, namely, $(b-a)/v$.

But the initial delay will differ for each, being $(p_1-b)/v$, $(p_2-b)/v$, &c., the amount of this difference being $(p_2-p_1)/v$, &c.

If all the conductors constituting the bundle were perfectly insulated from each other, since all the E.M.F.'s would be in parallel, there would be no higher P.D. produced by the joint action of any number of conductors. But if, as is probable, the short-circuiting is considerable, though of undeterminable amount, it may be assumed provisionally that the effective P.D. between the leads varies directly according to some function of the number of active conductors in the bundle. The problem then resolves itself into one of summation.

The " duration " of the effect, so far as the wave-front is concerned, is counted from the beginning of the earliest to the end of the latest effect. Hence the duration must be dependent partly on the distribution of the points of origin in the several linear conductors constituting the bundle.

Each conductor, as it flashes into activity, keeps up the P.D. for a time given by $t = (b-a)/v$, but its contribution arrives early or late according to the position of P.

We may therefore write,

$$t_1 = (p_1-b)/v\,; \qquad t_n = (p_n-a)/v\,;$$

and

$$t_n - t_1 = (b - a + p_n - p_1)/v,$$

i.e., the duration is increased by an amount equal to the time required by the wave to traverse the whole length occupied by the points of origin.

The rise of P.D. will be more or less gradual, and so will its subsidence, although the actual changes in each constituent conductor are still supposed to be sudden and definite in amount. The effect of a gradual development of E.M.F. will be dealt with later.

It is manifest that the most favourable conditions for studying the distribution of the points of origin are when the leads are far enough apart to separate the two phases of the response by a zero interval.

(2.) With leads B and D, *i.e.*, on both sides of a group of points of origin, the case is different (see fig. 9).

By the same formula as before,

$$t_1' = (d - p_1)/v\,; \qquad t_1^n = (d - p_n)/v\,;$$

$$t_2' = (b - p_1)/v\,; \qquad t_2^n = (b - p_n)/v\,;$$

and the duration is comprised between the smallest and the greatest value of t.

Now if $\overline{P_nD} < \overline{BP_1}$ then is $\overline{BP_n} > \overline{P_1D}$.

For let $\overline{P_nD} = \alpha$, $\overline{BP_1} - \overline{P_nD} = \beta$, $\overline{P_1 - P_n} = \gamma$.

Then $\overline{BP_n} = \alpha + \beta + \gamma$, which is greater than $\overline{P_1D} = \alpha + \gamma$.

Hence in this case the total duration of the first phase, due to the wave-front, is governed by P_n the point of origin nearest to either lead, and the direction or sign of the P.D. depends on which lead it is nearest to.

From this it follows that if any two similar conductors, P_1 and P_m, in the bundle have their points of origin of E.M.F. situated at equal distances on either side of the middle point between B and D, they will neutralise each other, not only as regards the P.D. resulting from the development of the wave of E.M.F. in them, but also as regards the effect produced by its subsidence.

Similarly P_2 will neutralise P_{m-1}, and P_3 will neutralise P_{m-2}, so that no difference of potential will result save from the portion P_{m+1} . . . . P_n, *i.e.*, the points of origin not symmetrically situated between the leads B and D.

This consideration indicates a method which I have occasionally employed of locating the mean position of a group of points of origin.

(3.) With points of origin partly between and partly beyond the leads, as in fig. 10.

Here $\overline{B.P_n}$ is the longest distance, and therefore governs the superior limit of duration. But D itself is over a point of origin,

hence $p_d - vt_1 = d$ marks the beginning of the difference of potential, and this gives $t_1 = 0$. It should be noted that, as in the previous case, if any two similar conductors have their points of origin of E.M.F. situated at equal distances on either side of the middle point between B and D they will neutralise each other, and thus reduce the total P.D.

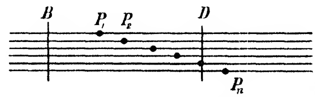

FIG. 10.—As in Fig. 9. B, D, electrometer leads. P_1 . . . . P_n, points of origin.

In fig. 11, p_1, from its position would add nothing to the P.D. until the wave-front starting from it had reached D on the one side. But its effect would cease the moment the opposite front of the wave reached B. The maximum would therefore be as intense as with all the points of origin outside the leads, but it would last a shorter time and appear to develop more slowly.

In this connection it may be observed that the form of the rise of potential difference between the leads B and A gives the distribution of the points of origin p_1, p_2, p_3, ... in the bundle, whereas the form of the rise of potential difference for the leads C and D gives the distribution of p_n, p_{n-1}, p_{n-2}, &c.

Furthermore, it is evident that the curve of the second phase, in all cases where the leads are far enough apart, must be a repetition, reversed, of the curve of the first phase, so far as it is conditioned by the distribution in the bundle of the points of origin, and that any difference between the first and second phases must be due either to interference through overlapping or to some difference, general or local, in the time relations of the development and subsidence of the wave of electromotive force, or of its rate of propagation. The analyses show that such a difference exists.

B. *Influence of the Rate of Development and of Subsidence of the E.M.F. at a Given Point of each Conductor in the Bundle.*

The possibility that the development of the E.M.F. at successive points of a single linear conductor may not be sudden but gradual, must also be taken into consideration.

The effect as regards the time relations of the difference of potential at the leads is in the main similar to that produced by a bundle of conductors in which the points of origin of the wave of electrical change are distributed over a definite portion of its length.

If the circumstances are such that the distribution of the points of origin cannot be determined, and if there is no means by which the electrical activity can be caused to originate at some definite point of

the bundle, then it does not appear that sufficient data are afforded by the electrometer records to discriminate between the effect of the non-coincidence of the points of origin, and of the gradual development and subsidence of the E.M.F. at any given point.

Inasmuch, however, as it must not be assumed that the rate of rise and rate of fall of E.M.F. are equal, *i.e.*, that the potential gradient at the wave-front is the same as that at the end of the wave, it becomes necessary to find some mode of representing the time relations of the variations of E.M.F. at any given point of a single linear conductor. For this purpose the following device may serve: Let each linear conductor be conceived as consisting of a number of parallel elements which flash into complete activity in succession, and remain active for a period not necessarily equal, after which each one in turn passes suddenly into a condition of rest; *e.g.*, let the conductor p_1 consist of parallel linear elements $\pi_0 \ldots\ldots \pi_n$ so that $\pi_1 - \pi_0$ is the small interval of time that elapses before the second element comes into action, and so on.

Then the time at which a difference of potential is derived from each of these elements in succession will be

$$t_{\pi_0}' = (p_1 - b + v\pi_0)/v, \qquad t_{\pi_1}' = (p_1 - b + v\pi_1)/v, \text{ etc.},$$

and the times at which these contributions to the total P.D. cease will be respectively

$$t_{\pi_0}'' = [p_1 - b + v(\theta + k\pi_0)]/v, \qquad t_{\pi_1}'' = [p_1 - b + v(\theta + k\pi_1)]/v, \text{ etc.}$$

If $k = 1$ the formula represents an equal rate of rise and fall of E.M.F. at each point of the conductor.

If $k < 1$ the fall is more rapid than the rise.

If $k > 1$ the rise is more rapid than the fall.

C. *Effect upon the Variations of P.D. when the Conductors constituting the Bundle are not all of the same Length.*

There yet remains a farther complication arising in the case of a non-regular bundle, of which some of the constituent conductors do not extend far enough to pass under both leads.

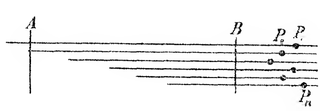

FIG. 11.—As in Fig. 9. A, B, electrometer leads. $P_1 \ldots\ldots P_n$, points of origin. But some of the linear conductors do not reach from B to A.

Let Q be the point at which a linear conductor ends, such that $OQ = q$, and following the notation hitherto employed, let $q_1, q_2 \ldots\ldots q_n$

represent the positions of the ends of the conductors in which a wave of electrical activity originates at the points p_1, p_2 . . . . p_n respectively.

Then, neglecting the function $f(\pi)$, which need not be here taken separately into account, the time of initial change of P.D. between the leads B and A will be $t = (p_1 - b)/v$ for the wave-front, which will continue moving onwards till $t_2 = (p_1 - q_1)/v$, where it will stop, so far as the conductor denoted by p_1 is concerned.

But the P.D. due to the wave-front in those conductors which do not reach the second lead, will not diminish until the tail of the wave, or subsidence of the E.M F., begins at the first lead. This will be when $t_1' = (p_1 - b + v\theta)/v$, and since this expression does not contain q, the second or electro-negative phase begins at the same time for regular as for non-regular bundles. But the second phase will end so far as the conductor denoted by p_1 is concerned when $t_2' = (p_1 - q_1 + v\theta)/v$, the relation $(p - q)/v$ determining whether there is zero between the phases or not.

It is evident, therefore, that in the case of a bundle of conductors some of which do not reach the second lead, the difference of potential due to the development of the E.M.F. will rise as rapidly as in a regular bundle, but will fall off more slowly, so that the first or electro-positive phase taken by itself may last longer and even be more intense.

But the second or electro-negative phase, due to the subsidence of the E.M.F. while beginning at the same time as in a normal bundle, will cease in each conductor as soon as it reaches q, causing the curve to tail off in proportion to the number of conductors which come to an end between A and B.

The function $f(\pi)$ merely rounds off the abruptness of the change.

III. *On the Interpretation of the Photographic Records.*

Gathering together the results of the preceding investigation, we find that the expression representing that portion of the P.D. due to the development of the wave of E.M.F. in the bundle is of the form

$$+\Sigma_A^B f(v, t, p, \pi, q),$$

and that due to its subsidence, is of the form

$$-\Sigma_A^B f(v, t, p, \theta, k . \pi, q),$$

the time relations of the total P.D. between A and B, being represented symbolically by the sum of these functions, taking t as the variable.

The object of the present investigation is to find out how far it may be possible under these exceedingly complicated conditions to determine

separately v, the velocity of propagation, p the distribution of the points of origin, θ the duration of the electromotive effect, π its rate of development, $k \, . \, \pi$ its rate of subsidence, and q the influence of conductors which do not reach the second lead.

As has been already stated, the problem is rendered more difficult by the fact that there must always be an escape of current within the bundle from one conductor to another, the amount of which cannot be determined.

Velocity of Propagation.

The function v, *i.e.*, the velocity of propagation, can, as is well known, be easily determined by varying the interval between P and B. This may be done by shifting B with respect to A, or by changing the position of P.

And the value of v may then be deduced by comparison of the records obtained before and after the change.

The comparison may be made either between the times at which the curve commences, or between the times at which the direction of the movement of the meniscus changes.

The commencement of the curve is sometimes difficult to detect, otherwise it would be the best to use, for it depends simply on $f(b, p, \pi)$, and so long as p_1 is greater than b (*i.e.*, the points of origin are all outside the leads) the delay of the beginning of the first phase is directly proportional to the time required by the wave to travel from P to B.

But if B is brought within the region occupied by the points of origin, there is a discrepancy owing to the fact that the rate of rise of P.D. is altered, and lessened.

The apex of the curve is frequently very well defined. It is sometimes referred to as marking the end of the first phase and the beginning of the second. This is approximately but not strictly true. The change of sign occurs a short but variable time after the change of direction of the movement of the mercury.*

Taking however the time of the actual zero P.D., which can be easily determined by interpolation on the derived curve, it is necessary to inquire whether this varies directly with the distance of B from P.

Zero P.D. is reached when

$$+\Sigma_{\mathrm{A}}^{\mathrm{B}} f(v, t, p, \pi, q) - \Sigma_{\mathrm{A}}^{\mathrm{B}} f(v, t, p, \theta, k \, . \, \pi, q) = 0.$$

Each term of this expression represents a series of values of P.D. forming a curve which is not symmetrical unless, among other conditions, the function $f(q)$ is absent.

* Hermann does not appear to have noticed that I had drawn attention to this fact in 1892. ('Phil. Trans.,' A, vol. 183, p. 103.)

But $f(q)$, whenever present, is conditioned by the position of A and B.

Consequently, if, to determine v, we compare the times of zero P.D. for different values of B, or of B and A, keeping P constant, the results will only be reliable if all the conductors of the bundle pass under A and B in both positions, but not otherwise, because then the shape of the second half of each curve will be altered, and consequently the time at which the ordinate of the second half of the curve of positive potential difference equals the ordinate of the first half of the curve of negative potential difference, will also be altered.

Hence, if the bundle of conductors is not regular in structure, v should be determined by keeping A and B constant, and varying P, the position of the exciting electrodes.

Having found v, a comparison of the lengths p, a, and b gives the true time t, and this compared with the measured time T shows whether there is any latent period S.

Influence of Temperature on Velocity of Propagation.

Is it possible by comparison of photographs taken at different temperatures, the position of the leads A and B and of the point of excitation P remaining constant, to determine the variation with the temperature of the velocity of propagation ?

Here again there are two parts of the curve that might be selected for comparison, viz., the commencement and the apex. It is necessary to inquire whether $f(v)$ is the only function likely to be changed so as to affect the result.

The commencement of the curve depends on $\Sigma_A^B\, f(v, t, p, \pi, q)$.

Of these, $f(v)$, the velocity of propagation, and $f(\pi)$, the rate of development, are the only functions that can possibly be affected by change of temperature. But it is equally certain that they are both so affected, the E.M.F. developing much more slowly at low temperatures. (See fig. 12.) The determination therefore of the actual commencement of the curve by extrapolation on the analysis is liable to an error which in practice is negligible above 7° C., but increases rapidly below that temperature.

In our present apparatus, which will be fully described in another paper, temperature is determined to 0°·03 C., or 0°·01 C. if necessary. The importance of this precaution is evident from fig. 12.

If the apex is taken as the point of comparison, the conditions are more complex, for at the apex

$$+\Sigma_A^B f(v, t, p, \pi, q) - \Sigma_A^B f(v, t, p, \theta, k \,.\, \pi, q) = 0.$$

This will depend not only on $f(v)$ and $f(\pi)$, but also on $f(\theta)$ and $f(k)$, both of which may be affected by temperature.

Unless, therefore, it can be shown that these functions vary so as to preserve the same relative values at different temperatures, the apex cannot be used for this determination on a single set of observations.

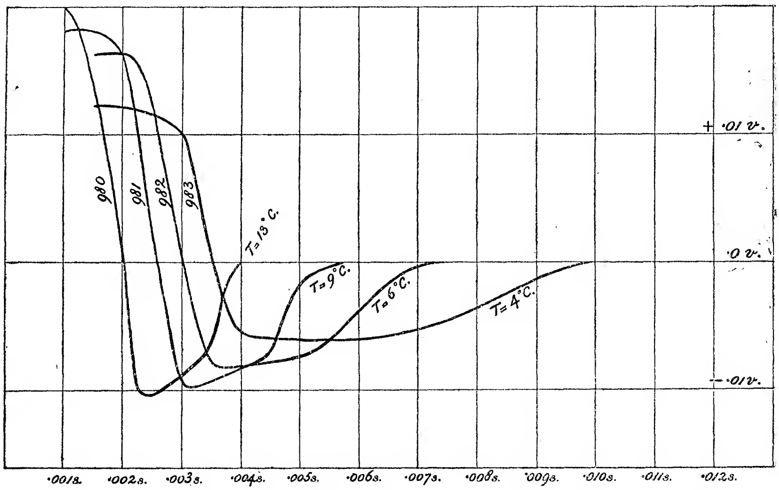

FIG. 12.—Influence of temperature on the response of a freshly prepared uninjured nerve. Electrometer leads 1 cm. apart, exciting electrodes 1·5 cm. from the nearest lead.

It should be noted that this method will not serve if the nerve is excited from the proximal end, because then $f(q)$ comes in.

If, however, the nerve is excited at two fixed points in succession at each temperature, keeping A and B constant, the effect of $f(\pi)$, $f(\theta)$, and $f(k)$ will be eliminated from the result, and only the function representing velocity of propagation will remain.

Functions affecting the Form of the Curve.

In the photographic records the total P.D. between the leads is given by

$$E = \alpha l + \beta . dr/d\theta,$$

where $l = r - R$ is the distance of the meniscus from its zero position R.

In the derived curves the values of E are plotted as ordinates with the corresponding values of time as abscissæ. Hence

$$dE/dt = \beta . d^2r/d\theta^2.$$

But by the preceding investigation it has been shown that, for the first phase,

$$\frac{dE}{dt} = f\left(\frac{dp}{dt}, \frac{d\pi}{dt}, \frac{dq}{dt}\right),$$

i.e., it is a function of three variables, namely, dp/dt, the number of linear conductors coming into action, $d\pi/dt$, the growth of the difference of potential at each point of each conductor, and dq/dt, the diminution of the number of active conductors between the leads owing to some of them not extending from P to A. Of these, dp/dt and $d\pi/dt$ can only be separated by such experimental methods as are tantamount to changing the distribution of the points of origin.

For instance, a muscle may be excited directly or by its nerve. In the latter case, the distribution of the points of origin is conditioned by that of the nerve endings—in the former case, by the disposition of the exciting electrodes. By a comparison of the results, a determination of $f(p)$ may be attempted, leaving, however, the uncertainty as to whether the altered mode of excitation may or may not have modified $f(\pi)$.

What may be termed the centre of gravity of the points of origin can easily be found on a gastrocnemius or sartorius by placing the leads one above and one below the nerve entrance, and shifting them till no excursion of the meniscus results on excitation.

Duration.

If the apex of the spike is very sharp and its beginning and end are gradual the analysis will show in many cases that the transition from maximum electro-positive to maximum electro-negative occupies about as long as the development of the first or electro-positive phase from zero. This is commonly met with in fresh muscle, especially gastrocnemius,* and fresh uninjured nerve.

It indicates that the duration of the active condition at each point is so related to rate of propagation, the development of the E.M.F. and its subsidence, the distribution of the centres of origin, and the distance between the leads, that the maximum slope of the wave-front (to make use of the other mode of expressing the problem) just reaches the electrode A as the maximum slope of the end of the wave passes B.

In other words, a sharp apex results from a particular relation between θ, v, p, k, π, and q, and the leads A and B, so that a sharp apex may become flat-topped from several quite different causes.

Flat-topped apices may be given by—

(1.) Kept nerves, especially at low temperatures.
(2.) Nerves which have been experimented on a great number of times.
(3.) Nerves under the action of CO_2. (See fig. 13.)
(4.) With leads further apart.
(5.) With leads closer together than usual.

* See my paper on the "Time Relations of the Capillary Electrometer," 'Phil. Trans.,' A, vol. 183, 1892, Plates 5 and 6.

It is very important to note that a flat-topped curve may indicate *either* that the wave of activity is so short compared with the distance between the leads, that its end has completely passed the first lead before its front has reached the second, *or else*, that the wave of activity is so long, that both leads are for an appreciable time included between its beginning and its end.

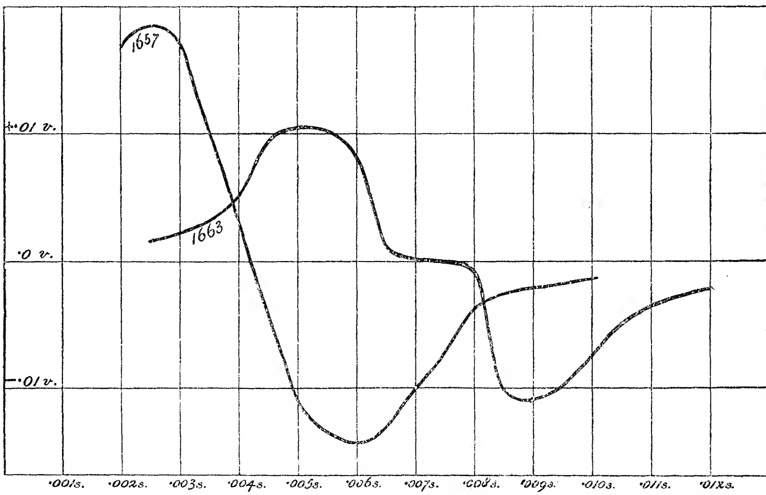

Fig. 13.—Effect of CO_2 on uninjured nerve kept 24 hours in tap-water saline No. 1657 = normal response in air, T = 4°·78 C. No. 1663 = response after CO_2, T = 4°·73 C. Electrometer leads 1·6 cm. apart, exciting electrodes 1·4 cm. from the nearest lead.

The most direct way of discriminating between the two cases is to alter the distance between the leads. If, with the leads farther apart, a sharper apex is produced, the wave is longer than from A to B. If, on the contrary, the length of the flattened summit is increased, the wave is shorter than the distance between the leads. An instance of this is given in fig. 14.

So far as the curves hitherto analysed have shown, both in kept nerves, and in nerve under the influence of CO_2, the length of the wave is relatively less than in fresh uninjured nerve. That is to say, the duration is not sufficiently increased to compensate for the slower rate of propagation.

In fig. 13 two analyses are given. One of these, No. 1657, is that of a nerve response under normal conditions. The apex of the photographed curve was sharp, indicating that the length of the wave was approximately equal to the distance between the electrodes, *i.e.*, 1·6 cm. The velocity of propagation, v, was 934 cm. per second.

The curve of which No. 1663 was the analysis, taken during the

action of CO_2, was flat-topped, indicating that the wave was shorter than the distance between the leads. Unfortunately, an exact determination of the velocity was not possible, owing to the great changes in the rate of development, $f(\pi)$. It may, however, be taken approximately as 467 cm. per second. This would imply a duration (θ) of 0·001713 second in both cases.

That is to say, the effect of CO_2 is to make the propagation rate slower, and the E.M.F. both smaller and slower in development, but not greatly to alter the duration of the maximum E.M.F. at any given point. With regard to the last clause, however, I propose to obtain more data.

Fig. 14 is an interesting set of analyses. The nerve, with the gastrocnemius attached, had been kept in tap-water saline for 20 hours. It was excited in the usual way, and the electrometer electrodes were placed for the first experiment, No. 1532, 21 mm. apart.

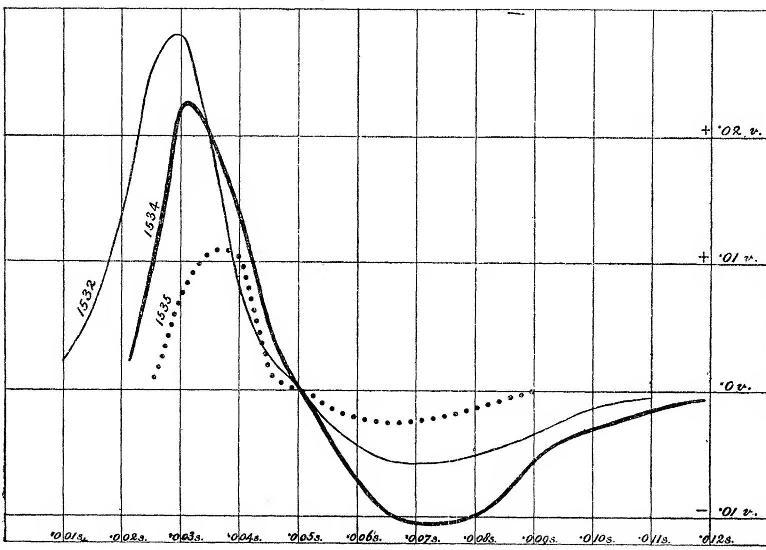

FIG. 14.—Uninjured nerve, kept 20 hours in saline. T = 4° C. No. 1532, distance between electrometer leads 2·1 cm. No. 1534, distance between leads 1·3 cm., approximately equal to length of excitatory wave. No. 1535, distance between leads 0·65 cm. Velocity 1055 cm. per sec. Duration about 0·00123 sec.

The proximal electrode was then moved 8 mm. nearer the distal, so that they were 13 mm. apart in No. 1534, and 6·5 mm. apart in No. 1535.

No. 1534 had a much sharper apex than either of the others, and the analyses indicate that the distance between the electrodes was greater than the length of the wave in 1532, and less in 1535. It may

be taken that the length of the wave was approximately 13 mm. The rate of propagation, v, was 1055 cm. per second, so that the duration (θ) was about 0·00123 cm. per second in this preparation.

In fig. 15 a similar preparation was used, but the nerve had been kept 48 hours.

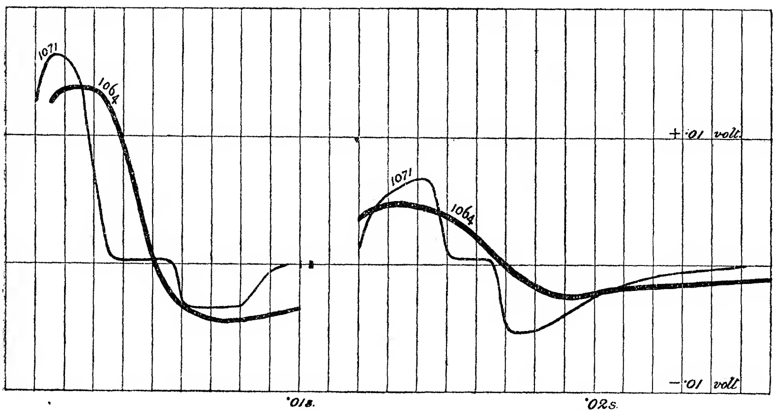

Fig. 15.—Influence of distance between leads on the time relations of the recorded electromotive changes. Nerve kept 48 hours. No. 1064, T = 4°·5 C., leads 2·3 cm. apart; second excitation at 0·0103 sec. No. 1071, T = 4° C., leads 0·8 cm. apart; second excitation at 0·01 sec.

On this occasion the proximal electrode was fixed, and the distal electrode was moved nearer to it, the distance between them being 23 mm. in No. 1064 (T = 4°·5 C.), and 8 mm. in No. 1071. It will be noticed that the curves in this case commence at the same time, whereas in fig. 14, when the proximal electrode was moved, they crossed the zero line together. The velocity, v, is about 1000 cm. per second, and the length of the wave about 2 cm., giving a duration θ of about 0·002 second, during which the electrical activity of each part in succession is at a maximum.

From the analyses it would appear that the period of development, $f(\pi)$, occupied 0·0005 second, and that of subsidence, $f(k.\pi)$ 0·0015 second, from which it may be inferred that this particular nerve would have been incapable of the smallest electrical response to a second stimulus during $f(\pi) + \theta = 0{\cdot}0005$ second $+ 0{\cdot}0020$ second, and only capable of a more or less feeble response during a farther period of 0·0015 second.

But although after about 0·0040 second the nerve might respond with full force, it by no means follows that a separate record would be given by the electrometer, for if the distance between maximum electro-negative of the first wave and maximum electro-positive of the

second exactly equals the distance between the leads, they neutralise each other, and the electrometer only records the electro-positive (first phase) of the first wave and the electro-negative (second phase) of the second, fusing them into a single response.

For the electrometer indicates in every case merely the algebraic sum of all the potential differences existing at any instant between the two leads.

Development and Subsidence.

Flat-topped curves are particularly valuable for determining the rates of development and subsidence of the electromotive condition at any given point on the nerve.

It is, however, necessary first to ascertain to which of the two classes mentioned above, the curve belongs.

(A.) Let the length of the wave be greater than the distance between the leads and let all the linear conductors pass under both leads.

Then both the beginning and the end of the first or electro-positive phase will be due to the wave front—passing first under the proximal and then under the distal electrode. The first phase of the photographed curve will therefore be sigmoid with the two ends similar as in fig. 16, *a*, and the analysis of it will be of the type shown in fig. 16, *b*, that is to say, symmetrical.

The second or electro-negative phase will be due entirely to the subsidence of the electromotive condition, first at the proximal lead, giving the beginning of the second phase, and then at the distal lead, corresponding to the end of the curve.

This phase also will be sigmoid with the two ends similar. The shape of each end will depend on two functions, one of which, $f(p)$, representing the distribution of the points of origin, is common to both first and second phase; but the other, $f(k, \pi)$, the rate of subsidence, is peculiar to the second phase.

I have come to the conclusion that in the great majority of cases the curves indicate a slower rate of subsidence than of development. The second phase of the photographed curve may therefore have under these conditions the form shown in fig. 16, *c*, and its analysis will be represented by fig. 16, *d*.

(B.) The second class of curve is produced when the length of the wave is less than the distance between the leads. In this case the beginning of the first phase and the beginning of

the second phase are both due to the development of the electromotive changes, and the end of the first phase and the end of the second phase to their subsidence. Thus a quick development and slow subsidence will be indicated for this class of curve when the end of each phase is more gradual than its beginning.

It is interesting to compare these results with those obtained by Professor Gotch and myself from Malapterurus.*

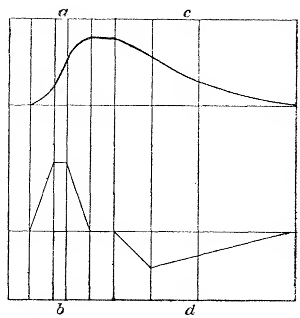

FIG. 16.—Diagram of record in which rate of subsidence is slower than rate of development. *a* = first phase of record; *b*, its analysis. *c* = second phase of record; *d*, its analysis.

Fig. 17 represents the analyses of three single shocks, the first of which was given when the preparation was fresh, and the third just before it ceased to respond to a stimulus. It will be observed that the development of the E.M.F. occupies from one-third to one-half the time required for its subsidence, and that the duration of the maximum is relatively short.

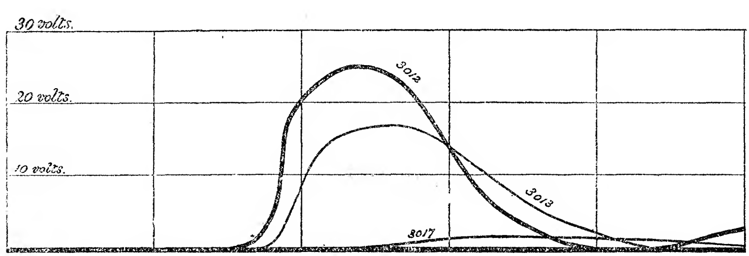

FIG. 17.—Analysis of three single shocks of piece of electrical organ of Malapterurus, taken at intervals of several minutes. T = 5° C. No. 3012, leads 1·5 cm. apart; No. 3013 ditto, but preparation failing. No. 3017, leads 0·2 cm. apart. Preparation ceased to respond after this.

* 'Roy. Soc. Proc.,' vol. 65, p. 439.

And analyses of other photographs—of which examples were given in our paper—show that no new development of E.M.F. takes place until the previous one is over.

The electrical phenomena of excited nerve and those of the electrical organ of Malapterurus are thus similar as regards these two points, namely, (1) the relative duration of development and of subsidence; (2) incapacity to show a second electromotive change while the first is in progress.

Farther confirmation is thus afforded of Professor Gotch's view, that the electrical phenomena of such fish are of nervous origin.*

Elimination of Fibres which do not reach the Second Lead.

The function $f(q)$ may be investigated by taking advantage of the fact that a nerve may be excited at either end. If two pairs of exciting electrodes are placed, one at each end of a long nerve, and a pair of electrometer leads between, as far apart as the length of the preparation will admit, the resulting curves will differ according to which end is excited. For when the electrodes at the proximal end are used, every fibre of the nerve is excited, but in the other case only those that reach the distal end are affected. Accordingly, the latter curve though smaller, is more symmetrical, and represents a simpler condition, from which $f(q)$ is eliminated.

When the proximal end is excited, as in the majority of experiments, the results are curiously complicated by conditions depending on the rate of propagation, the distance between the electrodes, and in addition their actual position on the nerve. For the ends of the fibres are not evenly distributed along the nerve, but occur in groups wherever a branch has been cut, and the effect of some of these groups can occasionally be distinctly recognised in a series of curves from the same preparation.

When the distal end is excited the resulting curves confirm the conclusion arrived at from my analyses that the development of the E.M.F. at any point is more rapid than its subsidence. A typical illustration of this is given in fig. 18, the analysis of the response of a kept nerve, with leads 3·1 cm. apart, at a temperature of 5° C.

A complete interpretation of this analysis cannot be given, as the commencement of the response is masked by the movement of the meniscus due to escape of the exciting induction shock, and there are not sufficient data to determine the rate of propagation, v, with accuracy.

But from other examples it may be inferred that the length of the wave was less than the distance between the electrodes. This is con-

* See Schäfer, 'Text Book of Physiology,' vol. 2, Article by Gotch, "On the Physiology of Electrical Organs," p. 591. Edin. and London, 1900.

firmed by the shape of the curve, which shows a zero pause of about 0·0005 second, during which time the wave must have been wholly between the electrodes.

Accordingly the rise of the electro-positive potential difference is due to the passage of the wave-front (development of E.M.F.) past the first electrometer lead, and the fall of it to the end of the wave (subsidence of E.M.F.) passing the first lead.

Similarly the first part of the second or electro-negative phase is due to the arrival of the front of the wave at the second lead, and the second part to the cessation of the E.M.F. under the second lead. Hence it may be inferred since (q) is eliminated, that the distance from maximum electro-positive to maximum electro-negative represents the time

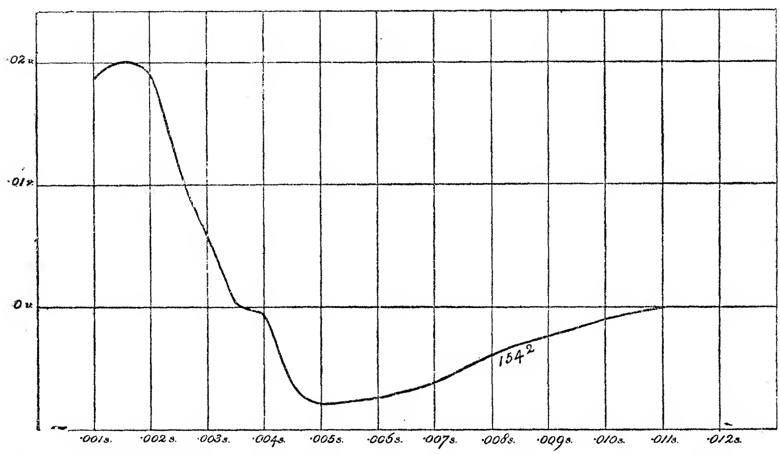

Fig. 18.—Nerve excited at distal end to eliminate effect of nerve fibres which pass only under one lead. T = 5° C. Leads 3·1 cm. apart.

required for the response to travel from one lead to another. This gives a velocity, v, of about 1000 cm. per second, and since there is a zero pause of at least 0·0005 second, the whole wave of electrical response from beginning to end cannot have been more than 2·6 cm. long, and the duration of the electrical effect at each point may have been about 1/400 second.

It should be noticed that the first part of the electro-positive phase and the first part of the electro-negative last a much shorter time than the end of the electro-negative and the end of the electro-positive. This agrees with what has been already stated about the rapid development and slow subsidence of the E.M.F. The shape of the second phase indicates that the nerve had been slightly injured near the proximal lead. The smaller E.M.F. is partly accounted for by the fact that although f (q) is eliminated, the *short-circuiting due to the*

unexcited nerve-fibres which surround the active fibres near the proximal end, shunts part of the current.

This curve should be compared with No. 1535 in fig. 14, in which the wave of electrical response is *longer* than the distance between the leads, and consequently the first phase is due entirely to the development, and the second to the subsidence, of the E.M.F.

The material discussed in this paper consists mainly of some 1900 photographs of the electrical response of nerve, taken in the Physiological Laboratory, Oxford, by Professor Gotch and myself. I have made full analyses of more than 150 of the curves, and have measured the principal points of a much larger number.

Many other examples could be given, but I have in each case selected the one best suited, either from the sharpness of the definition or the completeness of the data, to illustrate the theory. It has become evident from a comparison of the photographs, that the values of v, θ, π, and $k\pi$, are greatly affected by temperature and the condition of the preparation; but as these involve the physiological side of the problem, which will be dealt with by Professor Gotch, I have for the present confined myself to showing the methods by which they may be determined.

"Contributions to a Theory of the Capillary Electrometer. I.—On the Insulation Resistance of the Capillary Electrometer, and the Minimum Quantity of Electricity required to produce a Visible Excursion." By GEORGE J. BURCH, M.A. Oxon., F.R.S., Lecturer in Physics, Reading College, Reading. Received April 17,—Read May 1, 1902.

What may be called the Insulation Resistance of the capillary electrometer is important for two reasons—first, as to its bearing on the theory of the instrument, and secondly, as affecting the method of using it in dealing with electrical charges or quantities of limited amount. I propose briefly to record some of my own experiments on this head.

In many capillary electrometers, if an excursion of the meniscus is produced by touching the terminals with a source of electromotive force and then removing it, leaving the circuit open, the meniscus returns in a comparatively short time to the position it would occupy if the instrument were short circuited. In other words, the charge, which, as Lippmann showed, is contained in the instrument as long as the meniscus is deflected from its zero position, gradually leaks away. The question naturally arises, whether this leakage is accidental like